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A MIOCENE TOAD FROM COLOMBIA, SOUTH AMERICA

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The fossil toad described here is part of the large vertebrate assemblage of the La Venta fauna (Fields, 1959), and was collected by R. W. Fields during the 1949 University of California field expedition to the upper Magdalena Valley, Huila, Colombia, South America. It is the same specimen identified by D. Savage (1951) as a leptodactylid, cited by Estes (1961) as a bufonid close to the living *Bufo alvarius* and *B. crucifer*, and discussed briefly by Tihen (1962b, p. 14) as *Bufo* sp., near *B. marinus*. Tihen's very useful paper on bufonid osteology (1962a) now makes it possible to give a much more accurate and clear-cut assessment of the relationships of this animal. Few fossil *Bufo* have been recorded previously from South America (Tihen, 1962b).

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Class AMPHIBIA
Superorder SALIENTIA
Order ANURA
Family BUFONIDAE
BUFO MARINUS Linnaeus

Referred specimen—University of California no. 41159, postorbital portion of skull, eight articulated vertebrae, both scapulae with articulating proximal ends of the humeri, both distal ends of humeri in articulation with proximal ends of radioulnae, two fragments from the region surrounding the acetabulum of the pelvic girdle, distal end of right femur, proximal ends of both tibiofibulae, distal extremity of right tibiale-fibulare, and two unidentified fragments. Two bone shafts which were collected at the same time, and have the same specimen number, are probably mammalian.

Horizon—University of California locality V-4517, Monkey unit, Honda group (Fields, 1959, p. 419, and fig. 2).

Age—Late Miocene.

Fauna—La Venta.

Preservation—The skeleton was apparently complete before exposure and erosion disarticulated and destroyed parts of it. The matrix is a silty mixture of claystone and sandstone, and the cavities have been filled either with this material or with calcite. In some cases, calcite or matrix have remained as endocasts of parts of the bones. Breakage has apparently been the result of erosion, and has occurred at the weakest and thinnest points.

The shoulder and elbow complexes are articulated in flexed positions, and the vertebral column has a slight ventral curve, similar in both cases to their positions in life in a normal resting position. It is possible that the toad died and was buried in such a position.

Description—The maximum width of the skull across the posterior arms of the squamosals is 39.5 mm. A height measurement of the skull taken from the dorsal extremities of the prootic part of the otoparietal (in *Bufo*, paired processes directly dorsal to the foramen for the ninth and tenth cranial nerves) to the parasphenoid-pterygoid suture is 10.0 mm. A ventral measurement along the median line from the exoccipital condyles to the posterior border of the sphenethmoid is 11.7 mm. In occipital view, the skull roof appears flat, except for the strong postorbital crests and suggestions of the supraorbital crests. The foramen magnum is about 65 per cent wider than deep, and the foramina for ninth

and tenth cranial nerves are prominent. Only the left columella is present and its tip was broken in handling. Its true length, as indicated in the figures, was taken from a photograph made before the breakage occurred. The prootic parts of the otoparietal are strongly ossified laterally and ventrally and form the ventral borders of strongly marked troughs for the columellae. The pterygoids

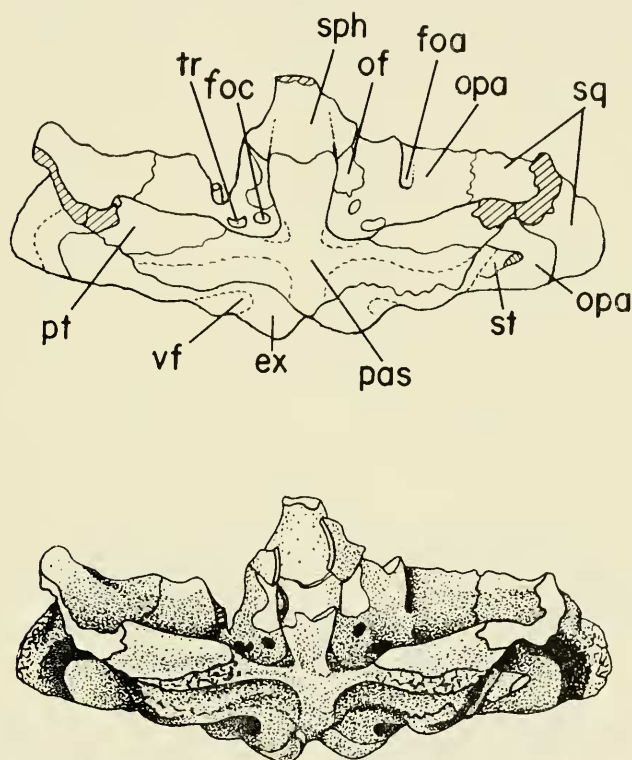


Figure 1. *Bufo marinus*, U. C. no. 41159, ventral view of skull, anterior to the top; above, outline, and below, shaded drawing; X2. On the outline, solid lines indicate sutures, dotted lines are contours, and cross-hatching indicates breakage. Abbreviations: *ecc*, endocranial cast; *ex*, exoccipital; *foa*, canal for occipital artery; *foc*, oculomotor foramen; *fom*, foramen magnum; *for*, foramen for maxillo-mandibular branch of trigeminal nerve; *fps*, frontoparietal suture; *ma*, attachment for nuchal muscles; *oc*, exoccipital condyle; *of*, large opening into braincase for optic and trochlear nerves; *opa*, otoparietal; *pas*, parasphenoid; *pt*, pterygoid; *sph*, sphenethmoid; *sq*, squamosal; *st*, columella auris; *tr*, foramen for fifth, sixth and seventh cranial nerves; *vf*, foramen for ninth and tenth cranial nerves.

are broken just medial to the point at which they would have given off their quadrate and palatal processes, and the descending quadrate processes of the squamosals are broken off at approximately the same level. The cultriform process of the parasphenoid is broken off just posterior to its juncture with the sphenethmoid, but the bone shows nothing unusual. The squamosal-prootic and prootic-parasphenoid sutures are difficult to discern, especially on the right side, and it appears that almost complete fusion has occurred.

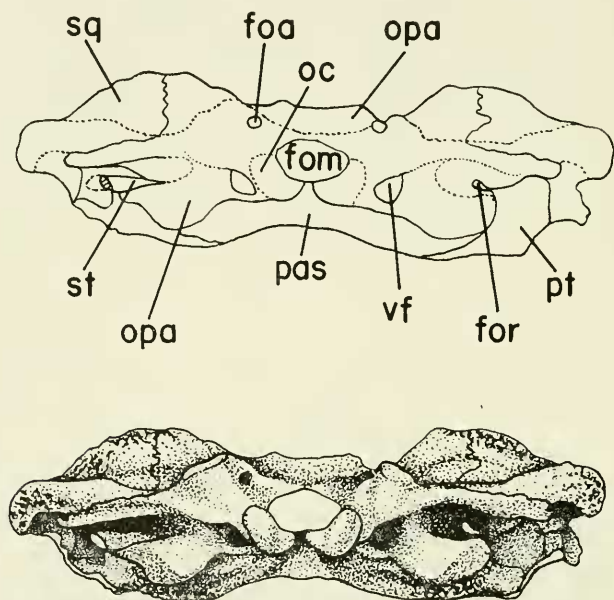


Figure 2. *Bufo marinus*, U. C. no. 41159, posterior view of skull; above, outline, and below, shaded drawing; X2. Comments and abbreviations as in Figure 1.

In dorsal view, the dermal ornamentation lacks strong protuberances other than the postorbital and orbital crests, though weak parietal crests are present, and two small bumps occur near the midline. The all-over pattern of the dermal ornament is a pitted and wrinkled one, in which the wrinkles extend more or less transversely across the top of the skull.

The frontoparietal portions of the otoparietals appear to be fused to each other, though an anterior groove, shown in Figure

3, perhaps indicates part of their suture. Conjoined, these frontoparietal areas are 21.7 mm. at their widest point. The anterior section of the frontoparietal area is broken off before its contact with the nasals. The occipital groove (Tihen, 1962a), is enclosed to form a canal. On the right side, breakage has removed the overlying bone and exposed the endocast of this canal.

In ventral aspect, much of the brain cavity appears as an endocranial cast. Small posterior fragments of the sphenethmoid, along with the anterior arms of the prootics and the cultriform process of the parasphenoid, completely surround an opening which was membrane covered in life and through which the optic

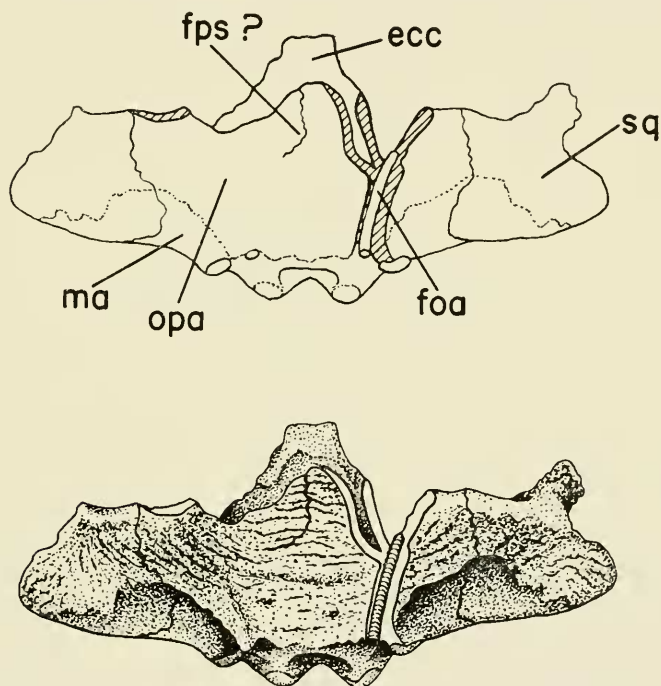


Figure 3. *Bufo marinus*, U. C. no. 41159, dorsal view of skull, anterior to the top; above, outline, and below, shaded drawing; X2. Comments and abbreviations as in Figure 1.

and trochlear nerves passed. This opening is somewhat squared-off, with notches in anterodorsal and posteroventral corners. Because of greater ossification, especially on the posterior border of the sphenethmoid, the opening is relatively smaller than that of

Recent *Bufo*. The lateral wings of the parasphenoid are broadly overlapped by rugose medial processes of the pterygoids. The foramen for cranial nerves five, six, and seven, and the oculomotor foramen are as in Recent *Bufo*. The occipital grooves (here enclosed to form canals) open on the ventral surface of the orbital portions of the frontoparietals, and are continued for a short distance as channels on the roof of the orbit. These paired canals, which in life transmitted the occipital arteries, diverge slightly as they pass anteriorly, but lie essentially parallel to the midline. Dorsal to the suture between the prootic and the pterygoid, immediately lateral to the foramen for cranial nerves five, six, and seven, and on a level with it, is a groove which passes through the prootic and emerges immediately lateral to the base of the columella. The maxillo-mandibular branch of the trigeminal nerve

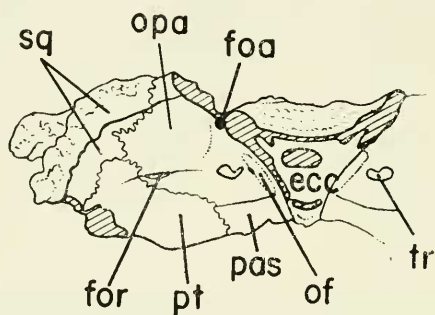


Figure 4. *Bufo marinus*, U. C. no. 41159, anterior view of right half of skull, outline only, showing posterior wall of orbit; X2. Comments and abbreviations as in Figure 1.

is found in this groove in *Rana* (Holmes, 1924, p. 296) and dissection showed this to be the case in *Bufo* as well. The groove in *Bufo* terminates on the lateral borders of the prootic, leading into the suprapterygoid fenestra (Tihen, 1962a, p. 160), but in this specimen there has been extremely high ossification in this area and portions of the prootic, squamosal, and pterygoid have completely closed the fenestra, and enclosed the groove in a foramen.

The thick and massive vertebral column is complete from the atlas back to about the level of the anterior third of the eighth vertebra, though all of the transverse processes are badly broken. The column was originally articulated with the skull, but was removed by the senior author in order to study the configuration of the exoccipital condyles and atlantal cotyles. An approximate

overall measurement of the seven presacral vertebrae is 42.5 mm. The atlantal cotyles are separated by a shallow notch. The neural spines are flattened and capped with dermal bone that has a slightly pitted texture. None of the broken transverse processes are long enough to give positive information about their true length or orientation, though they seem to have been oriented as in Recent *Bufo*. The zygapophyses are robust, as are the centra.

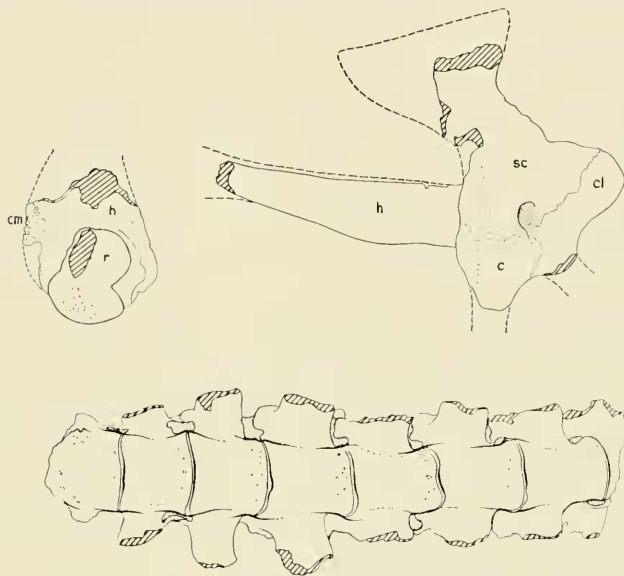


Figure 5. *Bufo marinus*, U. C. no. 41159, right, medial view of left scapula and humerus (*h*), showing sutural contacts of scapula (*sc*), coracoid (*c*), and clavicle (*cl*); left, anterior view of distal end of left humerus and proximal end of radioulna (*r*), to show *crista medialis* (*cm*); below, ventral view of vertebral column, anterior to left; all X2.

The right scapula is the better preserved. Its dorsal edge is broken parallel to, and near, the original natural border. The left scapula is broken at about the same point, but its posterior half is missing. In the glenoid fossa, the small band of cartilage that separates the scapula from the clavicle in the Recent species is completely replaced by a firm bony suture. In Bufonidae, the *pars acromialis* of the scapula (Proctor, 1921, p. 197) forms a strong prominence which is relatively larger in the fossil (on the right side; it is broken on the left) than in the Recent species. The

paraglenal cartilage (Ecker, 1889, p. 40), between the scapula and the coracoid, usually forms a noticeable portion of the floor of the glenoid cavity in modern anurans, but is absent in the fossil and replaced by a firm suture of these two bones. The large foramen in the glenoid fossa is, as a result of the heavy ossification in this region, slightly smaller than in the Recent forms.

The deltoid crest of the humerus is quite prominent, and is about as high from base to peak as the circumference of the humerus at the same point. The shafts of both humeri are missing, distal to the crests.

The radioulnar articulations are similar to those of Recent *Bufo*. On the distal segment of the left humerus, the *crista medialis* is well developed, and has a strongly rugose muscular attachment surface.

All that remains of the pelvic girdle is the ventroposterior corner of the ischium and a ventral piece of the ilium from near the acetabulum.

The proximal articulation surfaces and short segments of shafts of the tibiofibulae show no differences from Recent *Bufo*. The right tibiofibula has the longest shaft preserved. The grooves separating fused tibial and fibular components are deep but no more so than in the Recent species. The distal end of the right femur is no longer in natural articulation with the tibiofibula but still makes a perfect fit.

Both proximal and distal extremities of the right tibiale-fibulare are present. The diaphyses of the bones have been broken so that a natural fit is no longer possible.

Two small fragments may represent a posterior section of the ilial shaft and a section of tibiofibula, but are insufficient for positive identification.

Discussion—Tihen (1962a, p. 163) defines the *valliceps* species group of *Bufo* as follows: frontoparietals broad, usually produced into crests; roofing bones ornamented; occipital groove enclosed to form a canal; frontoparietals and prootics fused. He then divides the *valliceps* group into three essentially geographical subgroups: the Mexican section in Central and North America; the South American section in South and Central America; and the Caribbean section, throughout the Neotropical Region, "partaking to some extent of the characteristics of each of the others, besides developing its own features."

This fossil is placed in the *valliceps* group on the basis of presence of all of the above characters. Within this group, it is eliminated from the Mexican section by having a strong overlap of the

medial wings of the pterygoids onto the wings of the parasphenoid and complete closure of the suprapterygoid fenestra (*ibid.*, p. 168). The strongly-overlapping pterygoids are characteristic of the South American section, and do not usually occur in the Caribbean section, but the occluded suprapterygoid fenestra is present in the latter (*ibid.*, p. 171). This single resemblance to the members of the Caribbean section will be discussed below.

Bufo chilensis of the South American section and *B. retiformis* of the Caribbean section were the only species not available for this study. The dermal ornamentation of the fossil is most like that of the South American section, which has crests of only moderate extent and development and a lined or wrinkled sculpture; while crests in members of the Caribbean section are often extensive, exaggerated, and the sculpture is pustular.

A final factor used in allocating the fossil to the South American section was the width of the vertebral centra, which are perceptibly narrower in proportion to their length in the Caribbean group. As might be expected, the results are correlated with size, so that only specimens of relatively large size appear to be well separated. Many specimens of the Mexican section resemble the Caribbean forms in also having the narrow centrum.

The above considerations indicate that the fossil belongs to the South American section, but it differs from these forms in one characteristic of importance to Tihen's classification. He indicates (*ibid.*, pp. 165-166) that the suprapterygoid fenestra is not markedly occluded in the South American section of the *valliceps* group, while it is often nearly closed by flanges of pterygoid and squamosa in members of the Caribbean section. The fenestra is completely closed in the fossil, thus indicating a possible relationship to the latter group in terms of the classification based on skeletons of Recent species. However, the suprapterygoid fenestra, as a taxonomic character, may be weak in some cases (as Tihen realized), owing to its qualitative nature. Tihen points out (*ibid.*, p. 174) that *B. typhonius* of the Caribbean section lacks an occluded suprapterygoid fenestra. One specimen of *B. peltocephalus* of the Caribbean section (M. C. Z. no. 23564) also has an open fenestra. Within the South American section, one specimen of *B. paracnemis* (M. C. Z. no. 343) has the fenestra closed on one side of the skull. It is possible that closure of the fenestra in Recent specimens may be both variable within the species as a whole, and be partly a function of age of the specimen. In addition, since there has been a trend in many groups (including anurans) toward deossification, geologic age can be a modifying factor as well. The

latter is probably the most important with respect to this fossil, since a number of regions, e.g. shoulder girdle (see above) and prootic show a greater amount of ossification than comparable regions in any Recent specimen of either New or Old World *Bufo* seen by us.

The *crista medialis* of the humerus is of some interest in this specimen, because it is a secondary sexual characteristic in some Recent frogs. The *crista* forms the attachment for the *M. flexor carpi radialis*, which aids in flexing the wrist and is important in amplexus. Ecker (1889, pp. 42-43) indicated that the *crista* was present in males of *Rana esculenta*, *R. temporaria*, and *R. oxyrhinus*. Holmes (1924, p. 241), in discussing the same species, states that it is present in both males and females, but is more prominent in males. Inasmuch as the methods of embrace and courtship are more or less uniform throughout the Salientia (Noble, 1931, p. 111), this characteristic may be of similar significance in other anurans as well. Table I gives the results that were derived from specimens of *Bufo* related to the fossil.

TABLE I

Taxon	MCZ no.	sex	crista medialis
<i>B. peltocephalus</i>	29600	♀	absent
	23564	♂	present
<i>B. arenarum</i>	1263	♀	absent
	30650	♂	present
<i>B. blombergi</i>	29669	♀	absent
<i>B. marinus horribilis</i>	21439	♀	present but small
	29028	♂	absent — small specimen
<i>B. ictericus</i>	321	♂ ?	present

Only a small number of the M. C. Z. collection of New World *Bufo* were sexed at the time of skeletonization, and of the others, only a few have the ridge to any great extent. *B. marinus horribilis* (M. C. Z. no. 29028), a male which lacks the *crista medialis*, was the smallest individual of that species in the osteological collection and may not have reached maturity. The fossil is thus most probably a male, though exceptions such as the above render this uncertain.

SPECIFIC ASSIGNMENT OF THE FOSSIL

As indicated above, the specimen clearly belongs to the South American section. Tihen (1962a, p. 165) includes the following

species within this group: *Bufo arenarum*, *B. blombergi*, *B. chilensis*, *B. crucifer*, *B. ictericus*, *B. m. marinus*, *B. m. horribilis*, and *B. paracnemis*. The fossil differs strongly from *Bufo blombergi* in having strong supraorbital and postorbital crests. *B. arenarum* has very high cranial crests, which are rugose and slightly flattened on their dorsalmost surfaces, and has a relatively smooth skull surface between the crests—both characters in contrast to those of the fossil. *B. crucifer* has a sculpture pattern much finer in texture and more deeply incised than in the fossil, has strong parietal crests, and has a relatively smooth skull surface between the crests, as in *B. arenarum*. The remaining taxa are very closely related, and all have been included in a single undifferentiated species, *B. marinus*, by some workers, or treated as subspecies or full species by others. We have followed Tihen's taxonomy (1962a) for convenience in discussion. M. C. Z. specimens of *B. m. horribilis* indicate that this primarily Mexican group tends to have thin, fine, almost pitted sculpture, and relatively low cranial crests, unlike the fossil. Specimens of *B. ictericus* contrast with the fossil in having prominent parietal crests, though this is a variable character. Both skeletons of *B. paracnemis* available to us resemble the fossil in sculpture and crest pattern, but on each side have a very strong anterior angulation of the posterior skull margin, in contrast to the fossil and the other species included in the South American section, though the consistency of this character is not determinable at this time. Hence the strongest resemblance between the fossil and any Recent group, on the basis of the available specimens, is with *Bufo marinus marinus*. The tendency toward obliteration of sutures, the relatively greater ossification in prootics, suprapterygoid fenestra, and shoulder girdle, as well as the general robustness of some of the bones themselves, do not, in our opinion, warrant nomenclatorial recognition at the specific level, but merely reflect the often greater ossification seen in many fossils (discussed above on p. 9) and probably indicates a stage in the evolution of *Bufo marinus* in the broad sense. In identifying this specimen with the Recent *Bufo marinus*, we realize, with Taylor and Smith (1945, p. 541) and J. Savage (1960, p. 235) that the concept of *B. marinus* as currently used is a broad one, yet further refinement in the assessment of relationships of this fossil cannot precede re-evaluation of the Recent *Bufo marinus* complex.

The beginnings of such a re-evaluation have been provided by Bertini and Cei (1962), who studied the serological relationships

between some of the species involved. *Bufo marinus*, a predominantly Amazonian aquatic species, appears to be the most primitive type, and has given rise to xerophilic continental, and moisture-loving coastal populations in the southern half of the continent. Identification of this fossil with the populations usually referred to as *B. m. marinus* is thus consistent with the northern occurrence of the fossil within South America, and with the primitive nature of *B. m. marinus*.

Blair (1963, p. 11) has discussed evolutionary patterns in *Bufo*, and has suggested that the ancestral stock of the *marinus* group "somehow crossed into South America during its time of isolation from North America in the Tertiary." There is still insufficient fossil material to make any positive statement, but most recent work on fossil anurans suggests that by the late Cretaceous or Paleocene, family groups were well differentiated, and lines resembling many modern genera were already present. It is thus quite possible that the ancestral stock for the *marinus* group entered South America by a land connection with North America which persisted until late Paleocene time. If this is so, then it is not necessary to propose that they reached South America by some sort of "sweepstakes" method after the connection was severed.

SUMMARY AND CONCLUSIONS

A late Miocene toad from the upper Magdalena Valley, Huila, Colombia, South America, is referred to the Recent species *Bufo marinus*. Within this poorly understood group, it seems to show closest resemblance to *B. m. marinus* from northern South America. It differs from *B. marinus* only in having slightly greater ossification in the suprapterygoid fenestra, lateral parts of the prootics, and glenoid region of the shoulder girdle. This condition is insufficient evidence for recognizing a taxonomic difference from *B. marinus*, at least until restudy of the Recent forms is effected. The broad geographic and altitudinal range of the Recent species precludes ecologic interpretation. The species is aquatic, and common today along large river courses and may have been so on the Miocene floodplains as well. The fossil, in combination with the lizards described by Estes (1961), is another indication of the modernity of the herpetological elements of the late Miocene La Venta fauna, and of the greater extent of the floodplain-aquatic habitat in northern South America during the late Miocene.

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